Lack of evidence for pheromone-mediated secondary attraction in the fir engraver, *Scolytus ventralis* (Coleoptera: Scolytidae)

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ABSTRACT

To test the hypothesis that host selection and mass attack by the fir engraver, *Scolytus ventralis* LeConte, is mediated in part by pheromones, an exhaustive series of experiments was conducted. Gas chromatographic (GC) analysis and GC-electroantennographic detection analysis was performed on Porapak Q-captured volatiles from virgin and mated beetles of both sexes, logs of grand fir, *Abies grandis* (Dougl.) Lindl., with males, females or both sexes boring in the bark, and trees undergoing attack in the field, and on extracts of abdominal tips from beetles topically-treated with methoprene, a juvenile hormone analogue, or beetles boring in methoprene-treated bark of grand fir. None of these analyses disclosed any sex-specific compounds or compounds that changed markedly in concentration following treatment. Extracts of the females' terminal abdominal glands with associated vaginal palpi contained *exo*-brevicomin, a common aggregation pheromone in the genera *Dendroctonus* and *Dryocoetes*, but laboratory and field experiments showed it to have no apparent role in long-range orientation. Extensive visual and videotaped observations revealed that females walking on grand fir bark displayed apparent "calling" and "marking" behavior, and during courtship males rubbed the females' abdominal declivity with their frons, placing their antennae in juxtaposition to the females' vaginal palpi. These results are consistent with the alternative hypothesis that host selection and mass attack by *S. ventralis* are mediated solely by primary attractants from the host tree, but they do not rule out the possibility of short-range pheromone-mediated behavior.

Key words: *Scolytus ventralis*, Coleoptera, Scolytidae, chemical ecology, pheromones, host selection

INTRODUCTION

For over four decades, entomologists have investigated (and debated) the process by which the fir engraver, *Scolytus ventralis* LeConte, locates and colonizes its host trees, primarily grand fir, *Abies grandis* (Dougl.) Lindl., and white fir, *A. concolor* (Gord. & Glend.) Lindl. (Struble 1957; Vité and Pitman 1967; Ashraf and Berryman 1969; Berryman and Ashraf 1970; Ferrell 1969, 1971). We have recently produced conclusive

evidence for primary (host) attraction of *S. ventralis*, and demonstrated that attraction to traps in the field can be induced by a blend of 13 antennally-active volatiles from the bark of grand fir (Macías-Sámano *et al.* 1998). We argue that mass-attack by this species can be achieved solely through response to host volatiles. Part of this argument rests on an exhaustive series of experiments that produced no evidence for long-range secondary (pheromone-mediated) attraction in this species. Herein we present a summary of these experiments, and report some behavioral observations indicating the occurrence of close-range olfactory communication and courtship behavior.

AERATIONS OF BEETLES IN THE LABORATORY

Volatiles produced by groups of male, female or mixed sex *S. ventralis* were collected on Porapak Q following a standard aeration procedure (Macías-Sámano *et al.* 1998). Unless otherwise noted, the aerations were performed at 20 °C with a 12:12 h L:D regime; prior to aerations all insects were kept for up to 4 days at ca 4 °C in glass jars with moistened paper. Fresh grand fir logs were used as host material. In order to reveal possible variations in the volatile production by insects alone and/or insects plus host material, aerations were performed in the following sequence over 36 months.

1. Separate aerations of 104 unfed virgin females and 72 unfed virgin males in glass tubes (30 cm long and 3 mm diam.) for 312 h.
2. Aeration of 17 unfed virgin females and males in the same glass tube for 384 h.
3. Separate aerations for 168 h under darkness at ca 25 °C of bolts placed inside metal drums (70 cm long and 45 cm diam.), and attacked by 130 virgin females or 130 virgin male beetles introduced into preformed entrance holes.
4. Aeration of 130 females and 130 males boring together into a bolt under the above conditions for 120 h. Females were introduced into the bolts three days before the males.
5. Aerations of 154 virgin females or 236 virgin males individually boring for 96 h into grand fir logs inside glass aeration chambers (Macías-Sámano *et al.* 1998). All beetles had emerged the same day and were not cold stored. One uninfested control log (20 cm diam.) was aerated under the same conditions.
6. Aerations of 312 females and 175 males boring in grand fir bolts in separate glass chambers for 216 h, with Porapak Q volatile capture devices replaced with fresh devices after 60 h.
7. Above aerations repeated with 303 females and 120 males.
8. Aeration of 184 females and 106 males boring together (97 of each sex established pairs in galleries) in bolts inside a glass chamber for 192 h.
9. Aerations of males and females added daily to separate glass chambers containing grand fir bolts. First day, 84 females and 84 males. On days 2-4, 83 and 32, 163 and 79, and 38 and 13 males and females, respectively, were added. Aerations were conducted inside glass chambers for 288 h. All insects had emerged on the same day and were not cold-stored.
10. Aerations of 50 females and 50 males inside the same glass tube (as above) for 48 h. All insects had emerged the same day and were not cold-stored.

11. Aerations in glass chambers of beetles separated by a mesh from infested and uninfested grand fir bolts. First aeration: 50 females and 50 males in separate chambers with a screen-enclosed fresh uninfested grand fir bolt for 192 h. Second aeration: 25 males with logs infested by 25 females for 192 h. Third aeration: 26 females and 26 males in separate chambers boring into fresh grand fir logs (insects and bolts screen-enclosed), to which were added 26 females and 21 males, respectively, for 168 h. In this last aeration, the enclosed insects were placed on the logs two days before introduction of the other insects. Porapak Q volatile capture traps were replaced after 48 and 120 h.

Differential diagnosis (Vité and Renwick 1970) was carried out on male and female volatile extracts obtained in the different aerations to search for sex-specific compounds. Gas chromatographic (GC) analyses employed Hewlett Packard 5830A, 5880A, and 5890A instruments equipped with capillary inlet systems and FID. Fused silica columns (30 m x 0.25 or 0.32 mm ID) coated with SP-1000 (Supelco, Bellefonte, Pennsylvania) or DB-1 (J &W Scientific Inc., Folsom, California) were used. Coupled GC-mass spectrometry (MS) employed a DB-23 column and a Varian Saturn ion trap. Helium was the carrier gas for GC and GC-MS. Differential diagnosis showed neither insect-produced nor sex-specific compounds.

These results were supported by coupled GC-electroantennographic detection (EAD) analyses (Gries 1995) with male and female antennae, of the captured volatiles from aeration 9. A Hewlett Packard 5890 A instrument equipped with a DB-23-coated fused silica column (30 m x 0.32 mm ID; J & W Scientific) was used. Responses from excised antennae were amplified by utilizing a custom-built amplifier with a passive low pass filter and cutoff frequency of 10 kHz. Compound identities were confirmed by comparison of their retention times and mass spectra with those of authentic samples. GC-EAD analyses also revealed no candidate pheromones. The only clear trend was to observe high quantities of antennally-active host volatiles from those aerations in which the insects were actively boring into bolts or branches of grand fir.

AERATIONS OF TREES IN THE FIELD

Field aerations were conducted in a mature *A. grandis / Acer rubrum* L. forest with well represented Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco (Steel and Gier-Hayes 1992), located 10 km North of Coeur d'Alene Idaho. Adapting the methodology of Browne *et al.* (1979), 1 m long sections of the bole of six standing grand fir trees (mean diam. at 1.3 m = 83.2 cm) under attack by *S. ventralis* were wrapped in a clear plastic sheet open at the top with the sealed bottom exiting into a Porapak Q volatile trap. Air was drawn at 1.5 L per min through the trap under vacuum from a portable pump connected to a power generator. Two unattacked trees ca. 3 m from the trees under attack were also wrapped and sampled as controls. The aerations lasted 49 ± 1.5 h.

GC analyses (conditions as above) of the captured volatiles showed no conspicuous differences between infested and uninfested trees, reinforcing the results of laboratory aerations. Comparative GC-EAD analyses of volatiles from one infested-tree and one control tree aeration showed no significant differences in antennal responses.

JUVENILE HORMONE TREATMENTS

Juvenile hormone (JH) and JH analogues are known to promote pheromone production in the following scolytid species: *Ips paraconfusus* (Lanier) (Borden *et al.* 1969; Hughes and Renwick 1977a; Chen *et al.* 1988), *Trypodendron lineatum* (Olivier) (Fockler and Borden 1973), *Pityogenes chalcographus* L. (Francke *et al.* 1977), *Dendroctonus brevicomis* (Hughes and Renwick 1977b), *Pityokteines* spp. (Harring 1978), *Scolytus scolytus* F. (Blight *et al. 1978),* and *D. ponderosae* Hopkins (Conn 1981). These results led us to test the hypothesis that if *S. ventralis* produces an aggregation pheromone, treatment of beetles with JH should disclose evidence of that pheromone.

Accordingly, female and male *S.ventralis* that had emerged from logs within the past 24 h, or were excised from the bark after feeding in fresh grand fir logs for 48 h, were topically treated with 1 μg or 10 μg of methoprene (isopropyl-11-methoxy-2, 6, 11-trimethyl-2, 4-dodecadienoate), a juvenile hormone analogue, in 1 μl of pentane (Fockler and Borden 1973; Pierce *et al.* 1986). Newly-emerged control beetles were treated only with 1 μl of pentane. Each treatment was replicated with 20 beetles. Treated beetles were individually placed in gelatin capsules attached to a suitable grand fir log under room conditions. The insects were excised from the bark after 24 h, sorted by treatment, and their entire bodies were immediately extracted in pentane. The extracts were filtered through glass wool and analyzed by GC as above. A second 20-replicate experiment was designed following a modification of the technique used by Chen *et al.* (1988), with 1 μg of methoprene or pentane applied just to the circular area of the log circumscribed by the perimeter of the gelatin capsule holding the beetle in contact with the bark. The beetles would contact or ingest the methoprene while boring into the log. Only unfed insects were employed and they were placed on the log 2 h after the methoprene was applied to the bark surface. Pentane treatments were used as controls. Extracts were obtained and analyzed as above.

In no instance did GC analyses of extracts from treated and control insects reveal any compounds that changed in amount as a result of JH treatment, nor were there any evident sex-specific compounds.

GLAND EXTRACTS

Because the terminal abdominal accessory glands with their associated vaginal palpi have been implicated in the production of α-multistrain by *Scolytus multistriatus* Marsham (Gore *et al.* 1977), we examined female *S. ventralis* for similar evidence of pheromone production. Abdominal tips of 289 female beetles that had fed in grand fir bark for 5 days were obtained by dissection. The abdominal tip was exposed by a gentle squeeze of the insect's body, removed from the body with microscissors, and immediately crushed in pentane. The presence of the accessory gland with vaginal palpi in 20 excised tips was confirmed by microscopic examination.

GC-EAD analyses using male antennae followed by GC-MS analyses revealed the presence of *exo*-brevicomin, *exo*-7-ethyl-5-methyl-6, 8-dioxabicyclo[3.2.1]octane, in trace amounts in the female abdominal tip extracts. *Exo*-brevicomin is an important pheromone in the genera *Dendroctonus* and *Dryocoetes* (Borden 1985; Camacho *et al.* 1993), and has not previously been found in *Scolytus* spp.

Laboratory bioassays and field trapping experiments (Macías-Sámano *et al.* 1998) revealed no behavioral effect of *exo*-brevicomin on *S. ventralis.* However, there could be a link between the fact that *exo*-brevicomin is present in the female abdominal tip and the

"marking" and "calling" behavior revealed by videotape analyses (see below). It is possible that *exo*-brevicomin serves as a short range cue for male *S. ventralis* to detect a site with females in the vicinity, acts as a courtship inducer, or an epideictic (spacing) pheromone (Prokopy 1981) that accounts in part for the non-random distribution of *S. ventralis* attack (Berryman 1968), or serves as an allelochemic that suppresses attack by potential competitors.

VISUAL AND VIDEOTAPED OBSERVATIONS

Laboratory observations were made on at least 40 beetles placed on cut bolts of grand fir and allowed to attack freely in the laboratory. Similar observations were made in the field from at least 80 individuals. Beetles that took flight during laboratory observations were replaced. When this behavior prevailed, the log was replaced because it was considered unsuitable. When a particular behavior was observed, the sex or sexes involved were determined.

The behavior of 20 beetle pairs was documented by micro-and macro-videotaping at 22 °C and ambient light during 20 h of taping. Twenty beetles of each sex were allowed to run freely and bore into fresh bolts (50 cm long and 15 cm diam) that were vertically (10 beetle pairs) or horizontally (10 beetle pairs) set on a laboratory bench (scenario 1). Ten more beetles of each sex were placed on one log (5 pairs) and on 10 green branches with needles (5 pairs), in which females (20 in the log and 20 in the branches) had been boring for 48 h (scenario 2).

We used a Panasonic solid state camera WV-CD 110, fitted to either a Karl Zeiss surgical microscope or to a 50 mm (1:2.8) SMC Pentax-A macro lens, coupled to a 50 mm Vivitar 2x macro focusing teleconverter macro, depending on the degree of magnification needed. The camera was connected to a Panasonic GX4, Multifunctional Video Cassette Recorder AG-195, and the image was monitored with a Panasonic Color Video Monitor CT-1330-MC. Illumination was provided by a cold-light source (Schott KL 1500).

Observations were also made in the field. On 2 July, 1996, five uninfested 1.3 m-long logs of grand fir were set up vertically in an open area of a grand fir forest near Coeur d'Alene, Idaho. When the first *S. ventralis* started to arrive at the logs, visual observations of boring, courtship, and mating activities were made from 0900 h to 1800 h for three consecutive days.

Scenario 1. Most of the beetles were very mobile and fast walking. Often when two individuals (sex not determined) approached each other a very brief "wrestling" occurred by rubbing their frons. After about 10 min on the log, many beetles appeared to select a spot where they would bore into the bark. At this time several females performed one of two conspicuous behaviors. The majority were extruding the tip of the abdomen and rubbing it on the bark as they walked in a zigzag fashion (Figure 1) that suggests a "marking" behavior as occurs in some moths (Swier *et al.* 1976; Colwell *et al.* 1978; Szocs and Toth 1979; Teal *et al.* 1981; West and Bowers 1994). Each marking bout lasted about 30 s, and was repeated several times for up to 5 min. The second pattern, displayed by only two females, may have been a variation of the previous behavior. These females extruded and raised the very swollen tip of their abdomens, and walked in a zigzag fashion, emulating moth "calling" behavior (Figure 1) (Turgeon and McNeil 1982; Alford and Diehl 1985; West and Bowers 1994). Such activity lasted < 30 s, and was repeated several times in 5 min. Both "marking" and "calling" were not disturbed by nearby beetles of either sex, and "marking" occurred whether the logs were placed

horizontally or vertically. The "marking" behavior was seen again when two females were exposed to 0.25 mg of bark oil in an olfactometer (Macías-Sámano *et al.* 1998). To our knowledge these two behavioral patterns have not been reported for any other bark beetle.

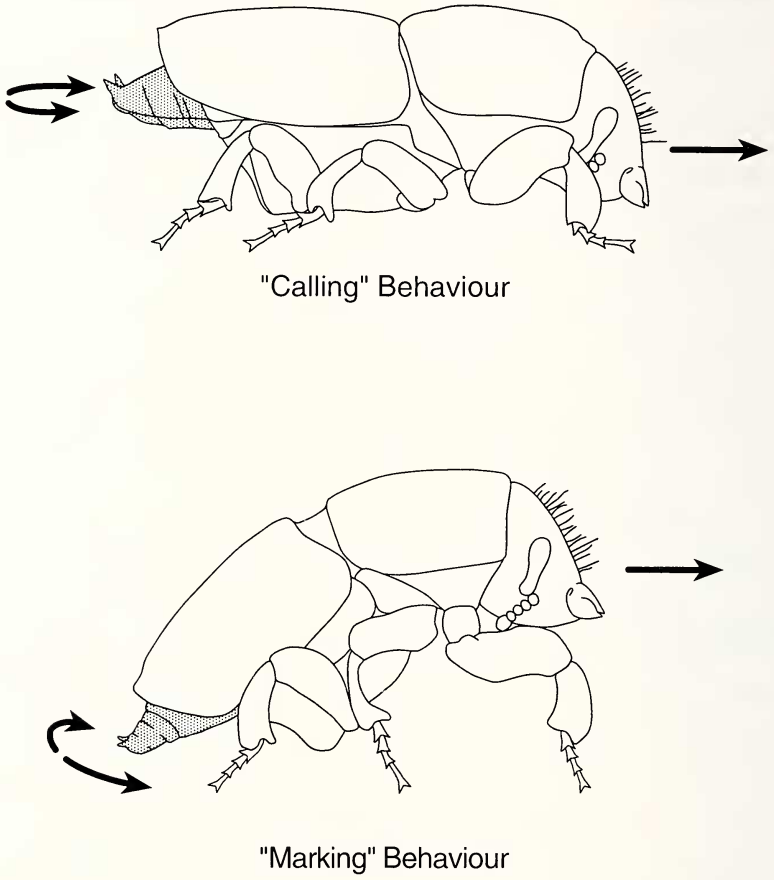

Figure 1. Apparent "marking" and "calling" behavior observed in videotape analysis of female *S. ventralis* with conspecifics on the bark of grand fir logs. Arrows indicate direction of locomotion and abdominal movements.

Scenario 2. All 10 females that had bored for 48 h into the bolt were observed in courtship and later in mating, as were the 10 females boring into branches, mainly at the twig crotches. The behavior was very similar to that found for *S. multistriatus* (Svihra and Clark, 1980), and confirmed the observations by Struble (1957) and Ashraf and Berryman (1969) for *S. ventralis*. All 40 couples mated outside the gallery, despite its length and the presence of a "nuptial" chamber, which is apparently used more as a turning area inside the gallery than for mating.

Each female waited within the gallery entrance facing inward. Courtship started when a male began to nod his head rhythmically against the abdominal declivity of the

female, possibly also stridulating. This action lasted up to 1 min and placed the male's antennae very close to or in contact with the vaginal palpi. The male then turned around and without inverting himself, as in some other scolytids (Francke-Grosmann 1951; Reid 1958), copulated with the apparently passive female who remained at the entrance. Defecation by females occurred frequently during courtship. Sometimes during courtship the males extruded their aedeagus once or twice, before initiating copulation.

In some cases a female arrived at an entrance occupied by another female, and apparently induced the resident female to leave, whereupon the intruder replaced her. On several occasions when a female was deep within a gallery, a male entered the gallery, and apparently enticed the female to the entrance by means of vigorous "nodding" on her abdomen, as also reported for *S. mali* (Doganlar and Schopf 1984). This episode required 2-4 min and was followed immediately by copulation.

All females copulated at least twice with the same male. In periods of observation up to 3 h long, no male remained with a female after the second copulation. Males copulated on average with three different females. Copulation lasted an average of 45 ± 3.5 s ($\bar{x}$±SE).

Field observations. Observations in the field confirmed the laboratory observations on courtship and mating behavior including the promiscuous behavior of both males and females. Two males were heard stridulating while in courtship. Rivalry displays between insects of the same sex were more pronounced, and females stole entrance holes more often. The speed at which 10 beetles walked up and down the logs was timed at 0.63 m per min. This walking speed, and the fact that the beetles never walked straight, suggest that *S. ventralis* could easily visit several trees a day, and assess their suitability as hosts as well as their occupancy by potential mates.

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